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A novel PDE model to describe terrestrial arthropods considering physiological age, reproduction rate, and body mass

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ABSTRACT
Modelling the life cycle of terrestrial arthropods at multiple trophic levels and their interactions with the surrounding environment aids to understand the evolution of the populations living in the different ecological niches. The need to predict the future *scenarii* in a precision agriculture and forestry framework is pushing even more the development of models that can support and be supported by measurements. Although the theoretical developments of the last decades provided interesting solutions, the growth in terms of biomass has still not been properly included in physiologically based models. Modelling the biomass component of insect populations is of wide importance, given the growing availability of measurement systems that provide the biomass reduction in agriculture and forest environments. This work, hence, proposes a novel physiologically based model describing populations of terrestrial arthropods considering time, physiological age, and biomass as independent variables. The theoretical formulation led to a partial differential equation describing the population dynamics which includes, as "*rate functions*", a series of sub-models that can be developed independently. These sub-models relate a specific aspect of the development of arthropods, mostly depending on the species, with the external environment and with the food resources available. A potential application to the case of the corn leafhopper *Dalbulus maidis* was considered as a secondary step of this study, to explore the model behaviour.

Section: RESEARCH PAPER

Keywords: Growth models; age structured models; functional response; trophic systems; applied mathematics

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1. INTRODUCTION

The mathematical description of populations of terrestrial arthropods, such as insects or mites, provides a synthetic representation of the biological mechanisms behind the development of the species, and how they relate with the external environment. Over the years, several models have been proposed and validated to describe the ontogeny of insect populations. Generally speaking, these models approximate the life stages with compartments [1]-[4] and can be clustered in different categories: phenological models [5]-[7], distributed delay models [8]-[12], individual-based models [13]-[15], and cohort-based models [16], to cite some examples. In each category, we can find different mathematical approaches. Without claiming completeness, the most common mathematical tools lie on the use of matrices such as the Leslie matrix [17]-[19], systems of ordinary differential equations [2]-[4], [20]-[26], and partial differential equations [27]-[33].

The complexity of the approaches is variable as well and ranges from the simple logistic-type growth curve [34] to some very complex models with dozens of parameters [35]. While the simpler models lack biological realism, their parameters are easier to calculate; more complex models lack generality, and their parameters are difficult to obtain [36]. Accordingly, more complex models may result in unreliable predictions because of the high dimensionality of the error matrix. Practical applications need models with biological realism, flexible parameterization, and that are simple enough to use with measurements. The latter aspect is always more important and cannot be neglected, given the increasing availability of measurement techniques in agriculture that can be helpful to update the estimation of the models and to increase predictions [37], [38]. A flexible parameterisation, instead, implies that the model, with few modifications, is still reliable even in the case some information is missing.

Although literature is full of reliable alternatives, and some of them consider the spatial variables as well (e.g., [39]-[43]), the great part of the models does not consider one of the fundamental aspects for the development of the insect species: the availability and the interaction with the host plant [44]. The host plant is a basic condition for the development of an insect species, as the amount of food ingested by the phytophages (and partially converted in body mass) strictly depends on its presence.

Some attempts of modelling the interaction between insects and host plants were carried out using the Volterra-Lotka predator-prey model [45], and all its further modifications (e.g. [46], [47]), or the functional response framework as common in ecology [48]. The effect of the food supply demand and the body mass increase, instead, was introduced by the metabolic pool model [49]-[51], which provided a first idea of how the food ingested is converted in energy and biomass by the organisms [52]. Gutierrez et al. [52] considered that part of the food is converted in energy needed, for instance, for respiration, motion, and reproduction. The remaining part of the food ingested is in part lost with the faeces and in part contributes to increase the body mass and size.

A population dynamics model describing a population developing over time and divided in age and size classes was introduced by Sinko and Streifer [32], [53]. Their formulation led to an extension of Von Foerster's equation [27], representing the population density $N(t, a, m)$ with three independent variables (time t, chronological age a, and body mass m), and where the flow of body mass is ruled by a specific growth rate function. A simplified version of the Sinko and Streifer model was widely applied to model fish populations. Temperature, in fact, seems to have a greater effect on fish body size and mass variations [54]. Aquatic environments and, more in general, the oceans are in fact subjected to lower temperature variations than the terrestrial ecosystems [55]. Accordingly, the definition of age class and body mass size is, in the case of aquatic ectotherms, often overlapped, leading to a modified version of the Von Foerster's equation where only time and body mass are considered [31].

However, temperature is not a negligible factor in describing the stage development of insect species and terrestrial ectotherms at large [57]. This is the reason why, over the years, different authors introduced a set of models, the *development rate functions*, that relate temperature and physiological age development [58], [59]. The relation between temperature and physiological age development in insect populations, moreover, led to the introduction of a novel formulation of the Von Foerster equation [28], [29] that has some similarities with the Sinko and Streifer equation [53]. The revised Von Foerster's equation considers the development of the individuals through the life stages driven by a specific development rate function. In the most general form, this rate can depend on time and physiological age, indicated by x to make a distinction from the chronological age a. This modification makes the Von Foerster's equation more suitable to describe insect populations, as showed by application in different case studies [60]-[63]. Hence, we have on the one hand a model valuable to describe the body mass development and, on the other hand, a model more suitable to describe insect populations because of the introduction of physiological age. In addition, the mathematical form of both the models is similar, and there are good preconditions to merge them in a more general model.

This work aims to merge the assumptions of Sinko and Streifer and [28], [29] to provide a general master equation that can be supported by other sub-models, describing: *i)* how the environmental parameters affect the development through the insects' life stages, *ii)* how the interaction between the species and the host plant can contribute to the growth, in terms of body mass, of the individuals. The practical application of the proposed model comes from the use of distributed measurement systems including mobile devices such as unmanned aerial and ground vehicles that, through suitable communication protocols [64] and synchronising procedure [65], will allow timely detection, identification, and quantification of pests.

Given this precondition, this study is divided into two parts. The first part presents the theoretical framework, the main objective of this study. The second part, instead, qualitatively explores the model considering the corn leafhopper *Dalbulus maidis* as case study. Notably, different simulations will be presented using: *i)* biological parameters retrieved by the literature, and *ii)* hypothesizing empirical values for the biological parameters not provided by the literature.

2. MATERIALS AND METHODS

2.1. Model description and assumptions.

The mathematical formulation of the model starts from the scheme already discussed in [28], [29], and [53]. The life cycle of an insect can be schematised with a series of chained boxes (Figure 1) where a cohort of eggs $R_0(t)$ enters the first stage, develops, and exits from the last box at the end of the life cycle. Each individual of the population, in addition, has a proper body mass value depending, as stated in Section 1, on diet, age, and food availability [66]. Accordingly, the individuals interact with the host plant in a different way, depending on the life stage. The host plant, in turn, provides nutrients that the organisms convert in energy [67] or body mass [52] (*de facto* increasing the size) depending on the needs [68]. Host plants, moreover, provide nutrients depending on environmental conditions and phenological stages [69], suggesting a dependence on time. The body mass is schematically represented by the third dimension of the box (Figure 1) and its effect provokes, in simple words, an inflation/deflation of the boxes.

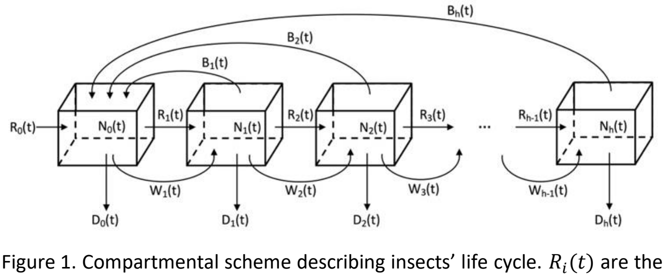

Figure 1. Compartmental scheme describing insects' life cycle. $R_i(t)$ are the flows of individuals entering or leaving the life stages, $D_i(t)$ are the flows of individuals leaving the life stages because of mortality, $B_i(t)$ are the flow of newborn individuals produced (theoretically speaking) by each life stage, $W_i(t)$ are the flows of body mass associated with the individuals entering or leaving the life stages and $N_i(t)$ are the number of individuals that at time t are in the *i*-th life stage. The list of the symbols is reported in Table 1.

Table 1. List and description of the symbols involved in the model description.

Symbol	Meaning	Measurement units
$R_{i-1}(t)$	Inflow of individuals entering from the previous stage at time t	individuals/day
$R_i(t)$	Outflow of mature individuals developing to the next stage at time t	individuals/day
$D_i(t)$	Flow of dead from the *i*-th stage at time t	individuals/day
$B_i(t)$	Flow of newborn, individuals that enters only the first stage at time t	individuals/day
$W_{i-1}(t)$	Inflow of body mass that enters the *i*-th stage at time t	kg/day
$W_i(t)$	Outflow of body mass that leaves the *i*-th stage at time t	kg/day
$N_i(t)$	Number of individuals in the stage *i* at time t	individuals
t	Time	days
x	Physiological age	age
m	Body mass	kg
$G(t,x,m)$	Development rate function	
$H(t,x,m)$	Growth rate function	
$M(t,x,m)$	Mortality rate function	
$\beta(t,x,m)$	Fertility rate function	
$N(t,x,m)$	Population density function: number of individuals per life stage and biomass class over time	individuals/(day·kg)

In the *i*-th life stage, an inflow of individuals, $R_{i-1}(t)$, enters the stage from the left side of the box, while an $R_i(t)$ flow of mature individuals exits from the right side. A specific function $D_i(t)$ expresses the flow of dead from the *i*-th stage, schematically reported in the bottom side of the boxes (Figure 1).

In line of principle, each life stage can produce a flow of individuals entering the first stage $B_i(t)$, namely the flow of newborn which have, by definition, physiological age zero and an initial value (defined) of body mass [22]. This flow is schematised in the upper surface of the boxes: it exits from each box, and it is directed towards the first block of the chain.

Given that each individual has a corresponding body mass value, the flow of individuals through the stages leads to a variation of the total body mass value of each single stage. This body mass flow is schematised in the front surface of Figure 1: an inflow of body mass $W_{i-1}(t)$ enters the stage of interest proportionally to the number of individuals and exits towards the next stage as $W_i(t)$. The number of individuals standing on the stage at time t is described by the function $N_i(t)$; moreover, it is worth remarking that all individuals have the same response to the surrounding environment [70].

The independent variables involved in the description of the population are time t, physiological age x, and body mass m. We can also assume that the increase of the variables x and m is slower with respect to time. This increase can be described by specific "rate functions" which mathematically express the relationship between the species and the external environment (e.g. physical factors or characteristics of the host plants), and describe the biological features of the species [12], [30], [71]. The rate functions can be defined as follows [72], [73]:

- The generalised development rate function $G(t,x)$ is the increase of physiological age x over time t:

$$\lim_{\Delta t \to 0} \frac{\Delta x}{\Delta t} = \frac{\mathrm{d}x}{\mathrm{d}t} = G(t,x) \tag{1}$$

- The generalised growth rate function $H(t,m)$ is the increase of body mass m over time t:

$$\lim_{\Delta t \to 0} \frac{\Delta m}{\Delta t} = \frac{\mathrm{d}m}{\mathrm{d}t} = H(t,m)\,. \tag{2}$$

The fertility $\beta(t)$ and the mortality $M(t)$ rate functions are assumed to depend, for the moment, only on time. It is worth remarking that the specific rate functions introduced above are general sub-models that can be developed independently, so that their mathematical form will not affect the model formulation that follows in the next section.

2.2. Model formulation.

Let us focus on a single stage having a duration Δx, in terms of physiological age, and a body mass range Δm (Figure 2). We aim to describe the variation of the individuals within the stage over time, namely $\frac{\mathrm{d}}{\mathrm{d}t}N^i(t)$. For this purpose, let us set a balance equation which considers: *i)* the inflow and the outflow of individuals in the stage, *ii)* the inflow and the outflow of body mass associated with each individual, that depends on the food consumption as well, *iii)* the total number of newborns produced by the individuals in the previous stages. Mathematically:

$$\frac{\mathrm{d}}{\mathrm{d}t}N^i(t) = R_{x-\Delta x} - R_x(t) + W_{m-\Delta m}(t) - W_m(t) - D_x(t) + \int_0^x B_x(t)\,dx'\,. \tag{3}$$

The dimensions of the equation (3) are respected if the body mass is expressed in "individual units": we can define how many kg/day correspond to the flux of individuals/day. This assumption can be obtained by *ad hoc* experiments that measure the average weight of each life stage of a given insect species with respect to the biomass ingested. The last term of the equation (3) describes the flux of newborns produced and leads to the "memory effect". In poor words, the model considers how the individuals produced by the previous generation affect the population abundance of the further generations [29].

To reshape the equation (3), let us introduce the population density function $N(t,x,m)$. The generalised development rate function (1) drives the development of individuals through the life stages, considering biology (e.g., ageing) and the relationship between the species and the external environment [70] (e.g., temperature). Accordingly, the fluxes $R_{x-\Delta x}(t)$ and $R_x(t)$ are

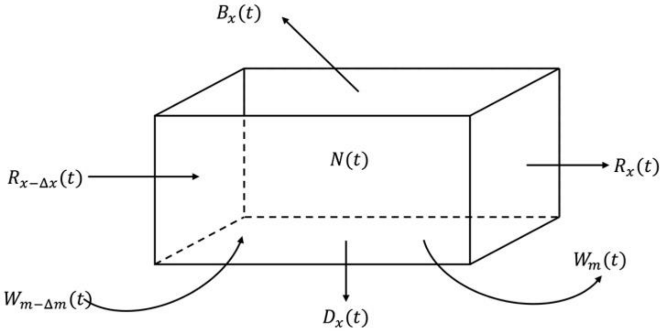

Figure 2. Schematic representation of a single stage. The list of the symbols is reported in Table 1.

directly proportional to the generalised development rate functions and to the population density function as follows:

$$R_{x-\Delta x} = G(t, x-\Delta x) \cdot N(t, x-\Delta x, m) \quad (4)$$

$$R_x(t) = G(t, x) \cdot N(t, x, m). \quad (5)$$

Analogously, the inflow and the outflow of body mass $W_{m-\Delta m}(t)$ and $W_m(t)$, respectively, are proportional to the generalised growth rate function (2) and the population density function. Similarly to expressions (4) and (5):

$$W_{m-\Delta m} = H(t, m-\Delta m) \cdot N(t, x, m-\Delta m) \quad (6)$$

$$W_m(t) = H(t, m) \cdot N(t, x, m) . \quad (7)$$

The same direct proportionality between the rate functions and the population density function can be considered for dead and newborns:

$$D_x(t) = M(t) \cdot N(t, x, m) \quad (8)$$

$$B_x(t) = \beta(t) \cdot N(t, x, m) . \quad (9)$$

The number of individuals on the stage $N^i(t)$ can be calculated by integrating the population density function $N(t, x, m)$ in the ranges $[x-\Delta x,\ x]$ and $[m-\Delta m,\ m]$:

$$N^i(t) = \int_{x-\Delta x}^{x} \int_{m-\Delta m}^{m} N\,(t, x', m')\, dx'\, dm' . \quad (10)$$

The terms (4)-(10) can be substituted into the balance equation (3) and divided by $\Delta x\, \Delta m$, obtaining:

$$\begin{aligned} &\frac{1}{\Delta x\, \Delta m} \frac{\mathrm{d}}{\mathrm{d}t} \int_{x-\Delta x}^{x} \int_{m-\Delta m}^{m} N\,(t, x', m')\, \mathrm{d}x'\, \mathrm{d}m' = \\ &= \frac{G(t, x-\Delta x) \cdot N(t, x-\Delta x, m) - G(t, x) \cdot N(t, x, m)}{\Delta x\, \Delta m} + \\ &+ \frac{H(t, m-\Delta m) \cdot N(t, x, m-\Delta m) - H(t, m) \cdot N(t, x, m)}{\Delta x\, \Delta m} + \\ &- \frac{M(t) \cdot N(t, x, m)}{\Delta x\, \Delta m} + \int_0^x \frac{\beta(t) \cdot N(t, x', m)}{\Delta x\, \Delta m} \mathrm{d}x' \end{aligned} \quad (11)$$

The terms of the equation (11) can be rewritten as follows:

- We can apply the mean value theorem for integrals to the first term of the equation (11) either to x or to m, obtaining:

  $$\frac{1}{\Delta x\, \Delta m} \frac{\mathrm{d}}{\mathrm{d}t} \int_{x-\Delta x}^{x} \int_{m-\Delta m}^{m} N\,(t, x', m')\, \mathrm{d}x'\, \mathrm{d}m' = \frac{\mathrm{d}}{\mathrm{d}t} N(t, x, m). \quad (12)$$

- We can rewrite the second term of the equation (11) considering the Taylor series expansion, in the x variable, of the function $G(t, x) \cdot N(t, x, m)$ truncated to the first order:

  $$\begin{aligned} &\frac{1}{\Delta m} \frac{G(t, x-\Delta x) \cdot N(t, x-\Delta x, m) - G(t, x) \cdot N(t, x, m)}{\Delta x} \simeq \\ &\simeq -\frac{1}{\Delta m} \frac{\partial}{\partial x} [G(t, x) \cdot N(t, x, m)]. \end{aligned} \quad (13)$$

  Manipulating the member on the right of (13)

  $$-\frac{\partial}{\partial x} \left[\frac{G(t, x)}{\Delta m} \cdot N(t, x, m) \right] \quad (14)$$

  it is possible to assume that

  $$\lim_{\Delta m \to 0} \frac{G(t, x)}{\Delta m} = G(t, x, m), \quad (15)$$

  namely that in the most general case the development rate is related to body mass. The expression (14) becomes:

  $$-\frac{\partial}{\partial x} [G(t, x, m) \cdot N(t, x, m)]. \quad (16)$$

- We can rewrite the third term of the equation (11) in an analogous way. In this case the Taylor series expansion is in the m variable and concerns the function $H(t, m) \cdot N(t, x, m)$,

  $$\begin{aligned} &\frac{1}{\Delta x} \frac{H(t, m-\Delta m) \cdot N(t, x, m-\Delta m) - H(t, m) \cdot N(t, x, m)}{\Delta m} \\ &\quad \simeq -\frac{1}{\Delta x} \frac{\partial}{\partial m} [G(t, m) \cdot N(t, x, m)] \end{aligned} \quad (17)$$

  and considering that

  $$\lim_{\Delta x \to 0} \frac{H(t, m)}{\Delta x} = H(t, x, m) \quad (18)$$

  the second term of (17) becomes

  $$-\frac{\partial}{\partial m} [H(t, x, m) \cdot N(t, x, m)]. \quad (19)$$

  The expression (18) underlines that there is a variation in body mass as the physiological age increases, as is it reasonable to suppose.

- We can rewrite the fourth term of the equation (11) considering that

  $$\lim_{\substack{\Delta x \to 0 \\ \Delta m \to 0}} \frac{M(t)}{\Delta x\, \Delta m} = M(t, x, m). \quad (20)$$

  In other words, variations in age and body mass can increase or decrease the mortality rate.

- We can rewrite the fifth and last term of the equation (11) analogously:

  $$\lim_{\substack{\Delta x \to 0 \\ \Delta m \to 0}} \frac{\beta(t)}{\Delta x\, \Delta m} = \beta(t, x, m). \quad (21)$$

  From (21) follows that

  $$\int_0^x \frac{\beta(t) \cdot N(t, x', m)}{\Delta x\, \Delta m} \mathrm{d}x' = \int_0^x \beta\,(t, x', m) \cdot N(t, x', m)\, \mathrm{d}x'. \quad (22)$$

The expressions (12), (16), (19), (20), and (21) provide the final version of the equation (11):

$$\begin{aligned} &\frac{\partial}{\partial t} N(t, x, m) + \frac{\partial}{\partial x} [G(t, x, m) \cdot N(t, x, m)] + \frac{\partial}{\partial m} [H(t, x, m) \cdot N(t, x, m)] = \\ &= -M(t, x, m) \cdot N(t, x, m) + \int_0^x \beta\,(t, x', m) \cdot N(t, x', m)\, \mathrm{d}x' \end{aligned} \quad (23)$$

Defined for $t \in (0, t^*]$, $x \in (0, x^*]$, and $m \in (0, m^*]$, where t^* is the maximum time considered in the simulation, x^* and m^* are the maximum age and body mass reachable for the species under study, respectively. Equation (23) needs initial and boundary conditions as well. The initial condition represents the initial population profile at time $t = 0$, that is the initial distribution of individuals in the life stages characterised by physiological age and body mass:

$$N(0, x, m) = \alpha(x, m). \quad (24)$$

The boundary conditions, instead, express the population trend over time and physiological age,

$$N(t, x, 0) = \gamma(t, x) \quad (25)$$

and the population trend over time and body mass,

$$N(t, 0, m) = \delta(t, m). \quad (26)$$

2.3. Model behaviour

2.3.1. *Dalbulus maidis* (DeLong, 1923) as case study

To explore the behavior of the model (23) we have chosen, as test species, the corn leafhopper *D. maidis*, an injurious pest specific for the *Zea* genus [74], [75]. Its life cycle has an average duration of 30 days in optimal temperature conditions, and it is composed of 7 identifiable stages: egg, five preimaginal stages, and adult. Recently, the partial differential equation (PDE) model [28] has been applied to describe the life cycle of *D. maidis* [62], providing a series of biological parameters contained into specific rate functions. The purpose of this section is to recall the results from [62] to explore the solution of the model (23) by randomly varying the input parameters.

The dependence of the corn leafhopper on the environmental conditions has been deeply explored by Van Nieuwenhove et al. [76], who provided the life tables. As a result, we could estimate the development rate functions, which relate the development of insects to the temperature of the living environment [57], [58], [59]. This dependence may be expressed by the Briére development rate function [77], as described in [62], mathematically defined as:

$$G[T(t)] = a\,T(t)(T(t) - T_{\mathrm{L}})\big(T_{\mathrm{M}} - T(t)\big)^{\frac{1}{m}} \text{ in } \frac{1}{\text{days}}\,; \tag{27}$$

T_{M} and T_{L} are the higher and lower thermal thresholds above and below which the development is theoretically not possible, respectively, while a and m are empirical parameters. The expression (27) leads to an unavoidable simplification of the development rate function $G(t,x,m) = G[T(t)]$; accordingly, the dependence of the development on both physiological age and body mass has not been considered. This simplification is reasonable for the following reasons: *i)* to date there is no information about the effect of ageing on insects' stage development, but this effect is negligible, *ii)* the body mass increase/decrease is already described by $W(t,x,m)$, and for the sake of this work providing too much complex expressions is not helpful.

Other biological information is included in the mortality, fertility and growth rate functions. To the best of our knowledge, there are no available expressions in the current literature to describe these aspects in the case of *D. maidis*, but we can introduce a series of assumptions. For the sake of simplicity, we considered the Hollings type II functional response [48] to describe the growth rate $W(t,x,m)$:

$$W(t) = \frac{a_{\mathrm{w}}\,P(t)}{1 + a_{\mathrm{w}}\,h\,P(t)}, \tag{28}$$

where a_{w} is the capability of *D. maidis* to finding and feeding on maize plants, $P(t)$ is the density of plants at time t, and h is the average search time. In other words, we assumed a direct proportionality between the body mass variation and the functional response which, in turn, describes the interaction between plants and pests. An additional simplification concerns $P(t)$, a_{w}, and h, that were considered constant.

Fertility, meant as average number of eggs produced by females over temperature, can be approximated by a Gaussian distribution centred in the optimal temperature value for egg production, T^*, and bounded by two temperature thresholds, which were assumed to be the T_{L} and T_{M} values within the Briére (27). Even though this assumption is not properly verified for *D. maidis*, it has been successfully applied to *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) and *Bactrocera oleae* (Rossi) (Diptera; Tephritidae) [2], [20], [62]. In mathematical terms, hence, fertility rate is:

$$\beta[T(t)] = \begin{cases} \gamma \cdot G[T(t)] \cdot \left[\dfrac{1}{\sigma_{\mathrm{T}}\sqrt{2\,\pi)}}\,\mathrm{e}^{-\frac{(T-T^*)^2}{2\sigma_{\mathrm{T}}^2}}\right], & \text{if } T_{\mathrm{L}} < T < T_{\mathrm{M}} \\ 0 & \text{otherwise} \\ & \text{[eggs/female]} \end{cases} \tag{29}$$

where γ is a normalisation parameter, $G[T(t)]$ is the Briére function (27), σ_{T}^2 the variance of the distribution. The function (29) has been multiplied by $G[T(t)]$ to consider adult longevity. Van Nieuwenhove et al. [76] estimated eggs production ranging from 13 to 40 °C with an optimal value $T^* = 33.61\ °\mathrm{C}$. The second parameter of (29) was set to $\sigma_{\mathrm{T}} = 7$, a value that covers a reasonable part of the whole oviposition range reported in [76].

As a last rate function, let us introduce the mortality $M(t,x,m)$. A good approximation can be obtained considering the so-called bathtub function [78], the following fourth order polynomial:

$$M[T(t)] = a_{\mathrm{M}}\big(T - T_{\mathrm{opt}}\big)^4, \tag{30}$$

where $T_{\mathrm{opt}} = 35.66\ °\mathrm{C}$ is the optimal temperature value calculated by (27) [62], and a_{M} is an empirical parameter. Notably, given that there is no information about mortality in *D. maidis*, a rough estimation of the value a_{M} just for model exploration purposes has been carried out considering that a mortality value close to 1 is reached when temperature reaches values close to T_{L} and T_{M}.

Since all the presented functions are temperature-dependent, we assumed regular periodic variations of temperature around a given value T_0, with amplitude A and period τ:

$$T(t) = T_0 + A \cdot \cos\left(\frac{2\,\pi}{\tau} \cdot t\right), \text{ in °C.} \tag{31}$$

The parameters involved in the rate functions have been randomly varied of a $\pm 5\ \%$ to explore the model response, except for T_0, A, and τ within (31).

2.3.2. Calculations

The values listed in Table 2 were considered as expected values of a Gaussian distribution. Simulations were carried out

Table 2. List of the parameters and respective errors considered in equations (27), (28), (29), and (30) for the model exploration in the case of *Dalbulus maidis*. Measurement units are indicated between square brackets only if available. The parameters that don't have any unit indicated are dimensionless.

Rate function	Parameter	Value
Briére development rate	a	$3.17 \cdot 10^{-5}$
(27)	T_{L}	9.00 °C
	$T_{\mathrm{M}}^{\mathrm{B}}$	38.99 °C
	m	3.07
Hollings type II functional response	a_{w}	$1 \cdot 10^{-5}\ \mathrm{m}^2$/individuals
(28)	h	0.004 s/individuals
	P	200 individuals
	γ	100 individuals/t
Fertility rate	σ_{T}	4 °C
(29)	T^*	33.61 °C
	T_{L}	13.0 °C
	T_{M}	40.0 °C
Mortality rate	a_{m}	$2 \cdot 10^{-5}$
(30)	T_{opt}	35.66 °C

on a set of 480 iterations corresponding to 480 model solutions. Each iteration provided for the following steps:

- Random parameters were generated from a Gaussian distribution having, as expected values, the values listed in Table 2.
- The deviation of the values generated in the previous step from the values listed in Table 2 is $\pm$ 5 %.
- The parameters generated in the previous steps were the inputs of the model from which the numerical solution was calculated.
- The previous steps were repeated for a total of 480 iterations.

Given that the parameters T_0, A, and τ within the temperature function (31) were not randomly varied, we explored the effect of the different temperature series considering three cases, summarized in Table 3. The Case I assumes a fixed period of oscillation τ and different values of T_0, while the Cases II and III aimed to explore different τ at two fixed T_0. All the cases explored had in input the same initial and boundary conditions, set, for the sake of simplicity, as follows:

$$\begin{cases} N(0,x,m) = 10 \\ N(t,0,m) = G[T(t)]. \end{cases} \quad (32)$$

Given the complexity of the equation, we explored the model using numerical solutions. The numerical scheme applied consists in a backward approximation of the partial derivative in x and m variables and in a forward approximation of the t variable [33], [73], [79], [80]. Given a sequence of values t_n, x_n and m_n, with the conditions $t_n < t_{n+1}$, $x_n < x_{n+1}$, and $m_n < m_{n+1}$, it is possible to define the discrete variables $i = t_{n+1} - t_n$, $h = x_n - x_{n-1}$, and $s = m_n - m_{n-1}$ [81]. Each variable increases of a step Δi, Δh, and Δs during the numerical simulation, to that $i = n \cdot \Delta i$, $h = n \cdot \Delta h$, and $s = n \cdot \Delta s$. With this precondition, we can obtain a discrete form of the equation (23):

$$\beta[T(t)] = \begin{cases} \gamma \cdot G[T(t)] \cdot \left[\frac{1}{\sigma_T \sqrt{2\pi}} e^{-\frac{(T-T^*)^2}{2\sigma_T^2}}\right], \text{if } T_L < T < T_M \\ 0 \qquad \text{otherwise} \\ \qquad [\text{eggs/female}] \end{cases} \quad (33)$$

In each simulation, $\Delta i = 0.1$, $\Delta h = 1$, and $\Delta s = 1$ were considered as integration steps, while the ranges explored were $t \in [0{,}360]$, $x \in [0{,}8]$, and $m \in [0{,}10]$. The numerical scheme (33) was implemented in a Python script publicly available at https://github.com/lucaros1190/Biomass-PDE, that entrusts functions within the packages numpy, scipy, pandas, and multiprocessing. This script allows the full reproducibility of the results presented in this study.

3. RESULTS

Proceeding by order, the first result of the model exploration is the Case I. The 480 simulations carried out for each combination of parameters T_0 and τ listed in Table 3,

Table 3. List of the parameters considered for the equation (31) for the model exploration. Note that $A = 1$ in the overall combinations listed in this table.

Case	T_0 / °C	τ / days
I – Fig. 3	20, 25, 30, 35	60
II – Fig. 4	35	1/120, 1, 30, 60, 90, 120
III – Fig. 5	30	1/120, 1, 30, 60, 90, 120

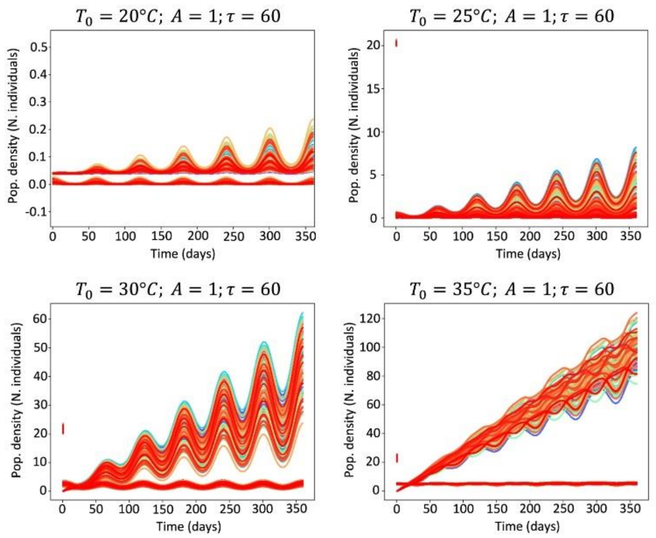

Figure 3. Results of the model exploration considering the parameters of the Case I. Different colours mean different simulations. Referring to (31), T_0 is the given temperature value, A is the amplitude of the oscillation and τ its period.

considering the random variations of the parameters listed in Table 2, are plotted in Figure 3. More specifically, the plots refer to the variation of the whole population in all age and body mass classes over time. Simulations showed an increase in the population density as T_0 increases, having a less regular pattern as the thermal optimum indicated by the Briére function (27) is approached. In all the parameter combinations plotted in Figure 3 the effect of the random variations of the parameters became relevant as time increases, showing how a small variation in the parameters provides relevant differences in the population abundance.

A different scenario is presented by the Case II, where T_0 and A were maintained constant around the optimum for *D. maidis* development, and τ varied according to the values in Table 3. The suitability of the temperature for the development caused a higher increase of the population in the overall plots reported in Figure 4. Independently from the value of τ, in fact, the Case II reported the higher population density, around 120 adults. The random variation of the parameters caused, in this case as well, relevant differences in the resulting population abundance, above all for large times. Simulations, moreover, highlight that solutions tend to a line as τ decreases, as shown by the first two plots in Figure 4. As τ increases, instead, the regularity of the shape of the solutions decreases.

The Case III is the case in which we observed the most regular shape of the solutions, as well as their higher variability. In this case as well, the solutions tend to a line as τ decreases (Figure 5), but, differently from the Case II, the loss of regularity as τ increases is not verified. This is a direct consequence of the dependence of the parameters on temperature: values close to the optimum reduce the effect of random variations of the parameters, but at the same time they decrease the regularity of the solutions.

4. DISCUSSION

This study introduced a novel PDE-based model that describes insect populations considering physiological age and body mass. The model is an extension of the well-known Sinko

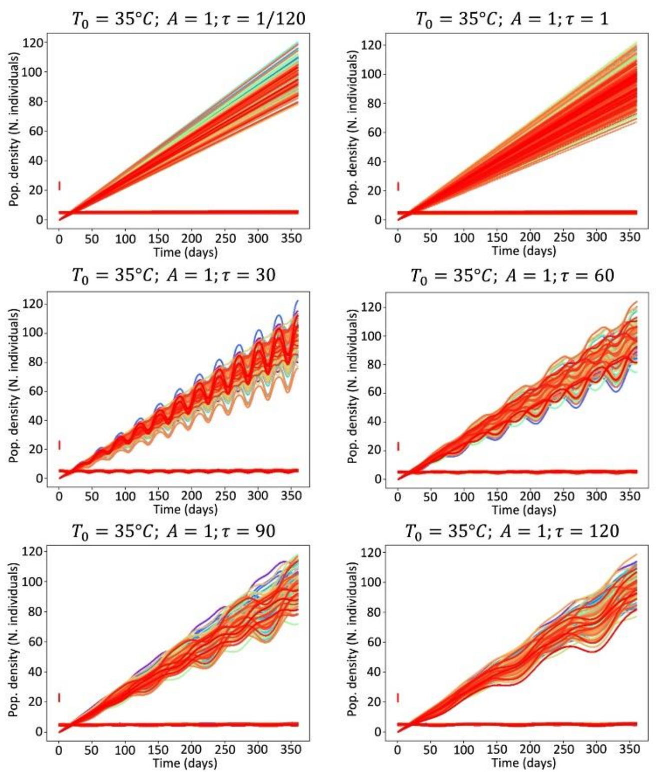

Figure 4. Results of the model exploration considering the parameters of the Case II. Different colours mean different simulations. Referring to (31), T_0 is the given temperature value, A is the amplitude of the oscillation τ its period.

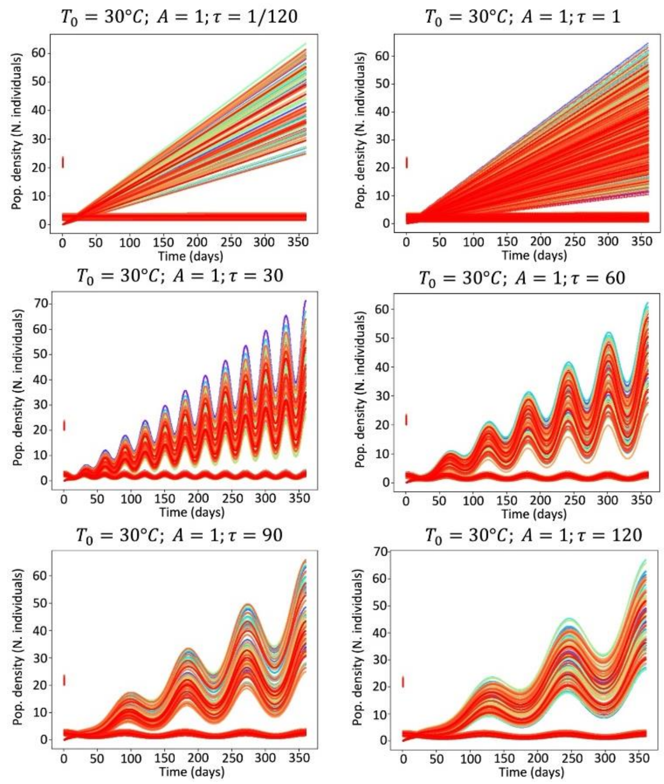

Figure 5. Results of the model exploration considering the parameters of the Case III. Different colours mean different simulations. Referring to (31), T_0 is the given temperature value, A is the amplitude of the oscillation τ its period.

and Streifer equation to the case of insects and terrestrial arthropods at large. It is in fact the first time, to the best of our knowledge, that a term indicating the physiological age is inserted into the Sinko and Streifer model. Our reformulation extends the classic body mass and chronological age dimension into body mass and physiological age. This extension is strategic, since it allows us to consider the development between the age classes driven by environmental and biological factors. Moreover, our formulation introduces an additional aspect of strategic relevance in modelling populations: the memory effect. Memory effect plays a fundamental role if the model is applied in DSS frameworks, above all to describe multivoltine species.

If $G(t,x,m) = 1$ the model (23) describes species that have no dependence of the development on temperature, such as an ideal homeotherm. In the literature there is a distinction in modelling terrestrial arthropods and homeotherms (e.g., [82] and reference therein), but equation (23) provides a generalisation in which both are special cases of a more general model. It is a great advantage from a theoretical point of view and lies in the flexible parameterisation that we mentioned in Section 1. It is worth saying, in addition, that flexible parameterisation is also endorsed by the possibility to insert a wide set of functions describing specific aspects, and that may be studied and formulated independently. Different authors are approaching, nowadays, to model formulations with this aim of generality (e.g., [2], [3], [38], [83], [84]) with a subsequent increase of stronger theories suitable to represent manifold ecological problems.

On the one hand, if the fertility function $\beta(t,x,m) = 0$ and $G(t,x,m) = 1$, the master equation (23) is reduced to the Sinko and Streifer model. On the other hand, the master equation (23), can be reduced to the model presented in [29] under the assumption that there is no variation in body mass. In other words, if $H(t,x,m) = 0$, it follows that $\frac{\partial}{\partial m}[H(t,x,m) \cdot N(t,x,m)] = 0$, and it is implicitly assumed that all the individuals of the population belong to the same body mass class, removing, *de facto*, the dependence on the variable m.

Two other examples of particular cases of the equation (23) are the model in [28] and the Von Foerster equation [27]. The former can be obtained if $\beta(t,x,m) = 0$ and $H(t,x,m) = 0$, while if we add $G(t,x,m) = 1$ to these two conditions, we obtain the latter, as well.

The generality of the model (23) has other additional advantages as well. Having the newborn directly into the master equation releases the initial and boundary conditions, that may be used to include different aspects of the biology and ecology of the target species. To give an example, initial and boundary conditions may include diapause/dormancy or eventual immigration/emigration of individuals, depending on the parameterisation of the model. Future works will possibly explore the features of the equation, starting from the results that have been reached in the Sinko and Streifer equation case over the years. Different authors (e.g., [32], [53], [85]) provided analytical solutions in particular cases (that may be obtained by the equation (23) under specific conditions), numerical schemes such as (33), or analysis on stability, existence, and uniqueness of the solutions.

Finally, as shown in the model exploration, the model (23) offers a flexible parameterisation without resulting in an excessively complex model, and its potential application covers a wide range of species of ecological and economic relevance.

At first sight, equation (23) seems to consider only a single trophic level. Instead, through an *ad hoc* formulation of the $H(t,x,m)$ function, it is possible to consider two (or more, in line of principle) trophic levels. This fact was highlighted by the model exploration, where a constant functional response was considered to describe the growth of the species in terms of body mass. Expressions such as (28) relate the growth rate and the abundance of the host plant with the ability of the pest species to find it. This is a relevant aspect to include in modelling populations in ecology: if in some cases the environmental conditions (e.g., temperatures, relative humidity, photoperiod) allow the development of a given species but host plants miss, the development of the insect population is not possible [86]. Most of the models currently involved in decision support system programs do not consider this fundamental aspect. The reason may be due to two implicit assumptions usually made for populations developing in cultivated fields: *i)* in cultivated fields there is an abundance of host plants (or food, more in general), and *ii)* the presence of the host plant is overlapped to the yearly pest populations development. However, these assumptions are not always verified, above all when the agronomic practices provide for an anticipation or a delay in the sowing or in the harvest. In that case the presence of the host plant is a determinant factor for the development of the species, above all if there is specificity between pests and crops. *Dalbulus maidis* is a species that lies in this pest category, since its presence is strongly related to the presence of maize [87], [88], [89]. The host plant affects survival and migration of the corn leafhopper [88]. Accordingly, in many areas of South America the presence of the species is not continuous over the year but strictly related to the periods when maize is cultivated [62].

It is worth remarking that the problem presented in the model exploration was partially based on biological data provided by the current literature, but the lack of information about how *D. maidis* advances in body mass classes, on mortality and fertility, required an unavoidable simplification of the problem, even though justified by the current literature. The low complexity of the scenario proposed for *D. maidis*, however, fitted with our purpose to qualitatively analyse the behaviour of the solutions without losing the connection with real case studies.

Overall, the model exploration underlined the behaviour on temperature and in case of parameters' variation. In real cases there is not a regular variation of temperature on time, but, at seasonal and daily scales, a periodicity in the measured values is assessed in the great part of the areas worldwide. The random variation of the parameters, moreover, can also be interpreted in key of experimental errors. The parameters of the rate functions, in fact, are usually estimated with data provided by *ad hoc* experiments, and hence affected by experimental errors or other types of uncertainties (e.g., statistical). While computing simulations, the estimated values are mostly taken "as they are" not considering, *de facto*, the experimental errors. The purpose of the model exploration that we presented was also directed towards a better understanding of the potential variation of the model output considering that the input parameters may vary in a certain range. The results leave to suppose that a small variation of the parameters correspond to a higher fluctuation in the population abundance as the temperature is far from the optimum of the target species. On the other hand, temperature values far from the optimum provide more regular solutions, a fact that does not happen otherwise and with a long periodicity of the temperature function.

In contexts different from agriculture, instead, the possibility to insert the host plant in a body mass model may support predictions, for example, of insect species of strategic importance for the ecosystems (e.g., [90] and references therein) or considered as indicator of their health status.

5. CONCLUSION

The next steps besides the present work will concern the validation of the theoretical framework hereby discussed. Analysing the feasibility of a validation, it is worth saying that most of the experimental trials usually employed in the case of insects, for instance, may be applied to equation (23). Parameters may be estimated with *ad hoc* laboratory experiments, such as the classical rearing of specimens at different constant temperatures [91], [92], [93], [94], but in this case more attention should be addressed to the body mass aspects. As already stated, the model (23) considers the growth rate of body mass in the most general way. In the model exploration we considered, for the sake of simplicity and exposition, this growth rate as a functional response, but it is possible to extend this part to more refined models as well. The main difficulty concerns the determination of the number of body mass classes that a given species may have, and if they may be clearly identified (such as insect stages). After this, a secondary step should concern the energetic aspects, to define the proportion of the biomass ingested by the specimens that is stored (with active increases of body mass) or transformed in energy. In a third step, the functional response may be involved to relate the species with the source of food, considering the ability of the individuals to find food, also.

The previous general considerations would be a purpose for future studies also to refine the usual experimental trials supporting the validation of the models. A great step forward on this aspect has been made in recent years, showing how the availability of data supports model development and *vice versa*. We believe that the model presented in this work may have large applicability in different contexts related to the biological, ecological and environmental sciences, also contributing to the modern vision of more sustainable control strategies based on information-control and forecasting.

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